

The Phenology of the Dryland Forest of Mauna Kea, Hawaii, and the Impact of Recent Environmental Perturbations

Author(s): Charles van Riper III

Source: *Biotropica*, Vol. 12, No. 4 (Dec., 1980), pp. 282-291

Published by: The Association for Tropical Biology and Conservation

Stable URL: <http://www.jstor.org/stable/2387700>

Accessed: 18/11/2008 12:01

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=tropbio>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



The Association for Tropical Biology and Conservation is collaborating with JSTOR to digitize, preserve and extend access to *Biotropica*.

# The Phenology of the Dryland Forest of Mauna Kea, Hawaii, and the Impact of Recent Environmental Perturbations

Charles van Riper III<sup>1</sup>

Cooperative National Park Resources Studies Unit, P.O. Box 54, Hawaii National Park, Hawaii 96718, U.S.A.

## ABSTRACT

The forest of Mauna Kea, Hawaii, was studied from 1973 through 1975 in order to define composition and phenology patterns of the two dominant tree species, and to determine the influence of man and feral mammals upon the ecosystem. There was a significant change in tree species composition across a 150 m elevational gradient; soil characteristics, drainage conditions, past disturbances by man, and browsing pressure by feral mammals are suggested as possible reasons. Although species composition varied with elevation, the tree density did not change. The phenological patterns of *Sophora chrysophylla* were found more closely tied to the weather pattern than were those of *Myoporum sandwicense*. Methods of pollination and seed dispersal were different between *Sophora* and *Myoporum*, and the spread of the latter is thought to be related to increased seed dispersal by recently introduced avian species, in conjunction with the limitation of *Sophora* reproduction due to browsing pressure by feral sheep. Because of the changes that are affecting the ecological organization of this community, the forest and its associated fauna need to be carefully examined in terms of present management policies.

ONE OF THE LAST REMAINING NATIVE DRYFOREST ECOSYSTEMS in Hawaii is composed of 12,000 hectares of high mountain savanna on the southwestern slope of Mauna Kea. *Sophora chrysophylla* (Leguminosae) and *Myoporum sandwicense* (Myoporaceae) are the most abundant trees, with scattered stands of *Euphorbia olowaluana* (Euphorbiaceae), *Santalum ellipticum* (Santalaceae), *Dubautia arborea* (Compositae), and two small plantings of introduced pine, eucalyptus, and cedar. Shrub and ground-cover species are considered elsewhere. No one has described the phenology of this forest although Hartt and Neal (1940) gave a species account of the vegetation on the eastern slope of Mauna Kea.

This ecosystem has been greatly influenced by the activities of man and introduced animals for the last 100 years (Warner 1960). Until the 1950's Parker Ranch grazed horses and cut *Sophora* for fence posts. Since the 1820's herds of feral sheep have roamed these volcanic slopes eliminating much of the *Sophora* reproduction by destroying the younger trees (Giffin 1976). Because of these perturbations, information was desperately needed on the present condition of the forest. This study was undertaken from April 1973 through August 1975 to compare forest composition and reproductive strategies of the two primary tree species (*Sophora* and *Myoporum*) in an effort to understand ecological interactions and influences on the forest as it exists today.

## METHODS

Study sites were selected on the southwestern slope of Mauna Kea at elevations of 1980, 2130, and 2290 m along the jeep road from Kilohana to Puu Laau (fig. 1). The 1980 and 2130 m sites were open to grazing by feral sheep, while the 2290 m study site was fenced on all sides. Five contiguous 30 x 30 m relevés, arranged in the shape of a T, were arbitrarily established near the center of each study site. All trees taller than 2 m (the height when *Sophora* and *Myoporum* first flower) were numbered, tagged, and, with the aid of a grid system, recorded on a map. Circumference at breast height (CBH) measured 1.4 m above the ground, was determined with a tape measure, and total tree height was measured with a clinometer.

Canopy density, flowering, and fruiting were measured monthly (see Lamoureux 1973, Frankie *et al.* 1974). Canopy density was determined by standing under each tree and recording the percentage of open sky observed. Flowering and fruiting were measured by estimating the number of available terminal branches on each tree, and recording the percentage of those that possessed fully opened flowers or mature ripe fruit. To offset the phenomenon of trees in one area being in heavy flower while 500 m away others lacked blossoms, every month I systematically walked across each study area outside the relevés, measuring the nearest tree each 30 m until 50 trees had been considered. These data were then added to those obtained from the relevés.

With the density of trees and intensity of flowering known, it was possible to extrapolate the yearly

<sup>1</sup>Present address: Department of Zoology and C.P.S.U., University of California, Davis, California 95616, U.S.A.

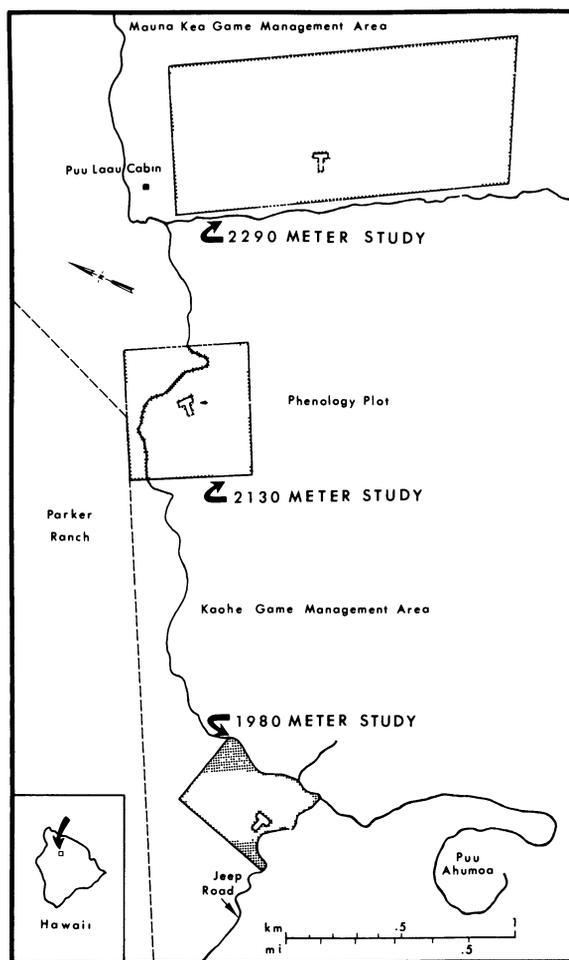


FIGURE 1. Map showing location of study area on the island of Hawaii, the study sites at 1980 m, 2130 m, and 2290 m, and the phenology relevés.

relative amount of flowering or productivity of each study location using the following formula:

$$P_j = I_j \cdot T_j \cdot M_j \cdot D_j \quad (1)$$

where,  $P$  = relative yearly flower production;  $j$  = elevation location;  $I$  = mean monthly percentage of flowering;  $T$  = total number of mature trees in all relevés;  $M$  = percentage of *Sophora* or *Myoporum* trees; and  $D$  = relative canopy size. Total fruit production ( $S$ ) for each elevation was calculated in the same manner except that percent fruiting ( $F$ ) was substituted for percent flowering ( $I$ ), giving the equation

$$S_j = F_j \cdot T_j \cdot M_j \cdot D_j \quad (2)$$

To take into account the variability in size among *Sophora* trees at each elevation, their mean circumferences were compared to that for trees at 1980 m;

CBH at 2130 m was 1.3 times as great and 2290 m was 2.0 times as great. This conversion was not necessary for *Myoporum* as the CBH was similar at all study sites. Weather data were collected at 2290 m; monthly temperatures were recorded with two maximum-minimum thermometers and rainfall with a National Weather Service rainfall gauge.

## RESULTS

**WEATHER.**—The daily weather pattern was usually predictable, with clear mornings and clouds forming about 1530 h. Temperature fluctuations between day and night were approximately 20°C, and although monthly high-low temperatures were similar throughout the year, there was a slight warming trend from June through October (fig. 2). Cloud cover during 1973 was sparse, and the range of recorded temperatures was larger than in 1974 or 1975.

The southwestern slope of Mauna Kea is in a rain shadow, and all the study sites were above the inversion layer. This meant there was much less rainfall, and lower humidity, than in other areas on the mountain. The average yearly precipitation from 1932 through 1972 was  $51.1 \pm 18.3$  cm; generally there was a pattern of high precipitation in December-January and in April, but yearly variances were great (fig. 3). The wet season usually extended from November to April and the dry season from May to October, although there was an unusual drought during 1973.

**FOREST COMPOSITION.**—Relative composition of the woods studied varied among the three study sites (fig. 4). At 1980 m *Sophora* comprised 48.2 percent of the forest and *Myoporum* 51.5 percent, at 2130 m *Sophora* abundance decreased to 26 percent and *Myoporum* made up the rest, and at 2290 m the forest consisted primarily of *Sophora* (91.5%) with *Myoporum* contributing only 8.2 percent. Because original numbers were percentages which varied extensively, I used an arc-sin transformation of the data (Snedecor and Cochran 1972); these differences at each elevation were significant (analysis of variance,  $P < 0.05$ ).

**TREE DENSITY.**—The number of *Sophora* and *Myoporum* trees at each elevation is given in table 1. The highest mean tree density (5.5 trees/100 m<sup>2</sup>) occurred at 1980 m; at 2130 m and 2290 m it was 4.0 and 2.5 trees per 100 m<sup>2</sup>, respectively. There was no significant difference in the density of trees (both species pooled) between elevations (one-way analysis of variance,  $P = 0.34$ ).

**TREE HEIGHT AND CIRCUMFERENCE.**—There was a

significant increase in tree height of *Sophora* at higher elevations, the trees averaging 1.7 m taller at 2290 m than at 1980 m (one-way analysis of variance,  $P < 0.01$ ). The circumference at breast height of

*Sophora* also increased with elevation ( $P < 0.05$ ), showing a mean difference of 48.5 cm between 1980 and 2290 m (table 3). *Myoporum* increased only 1 m from the lower to the upper study site (table 2),

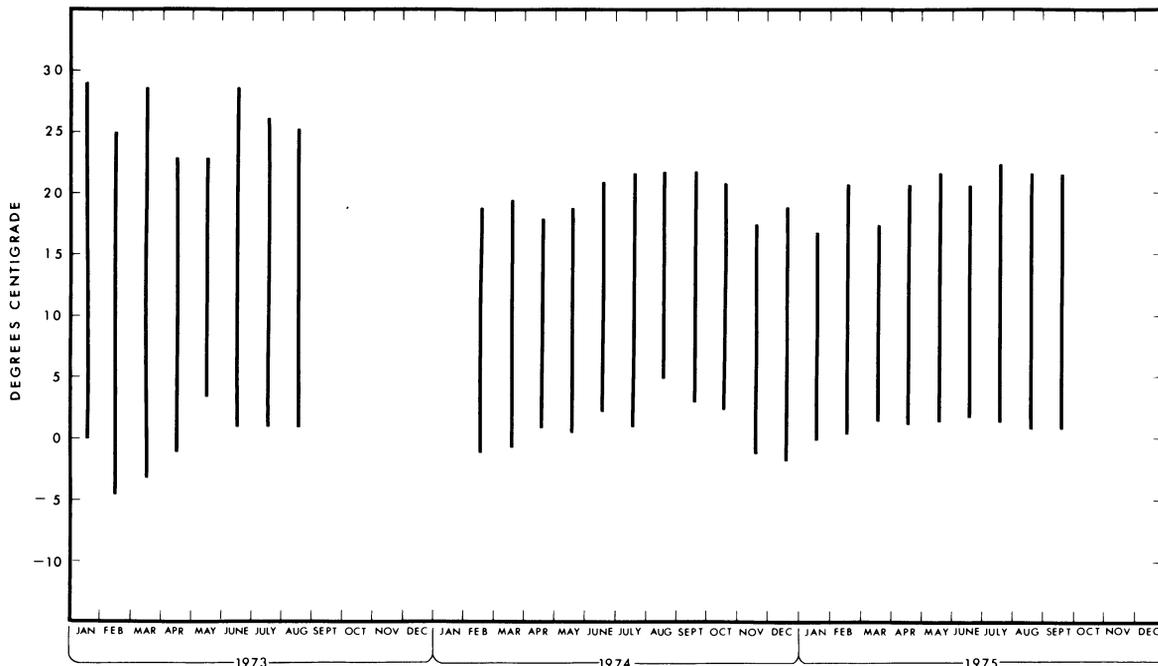


FIGURE 2. Monthly temperature ranges at 2290 m on Mauna Kea, Hawaii.

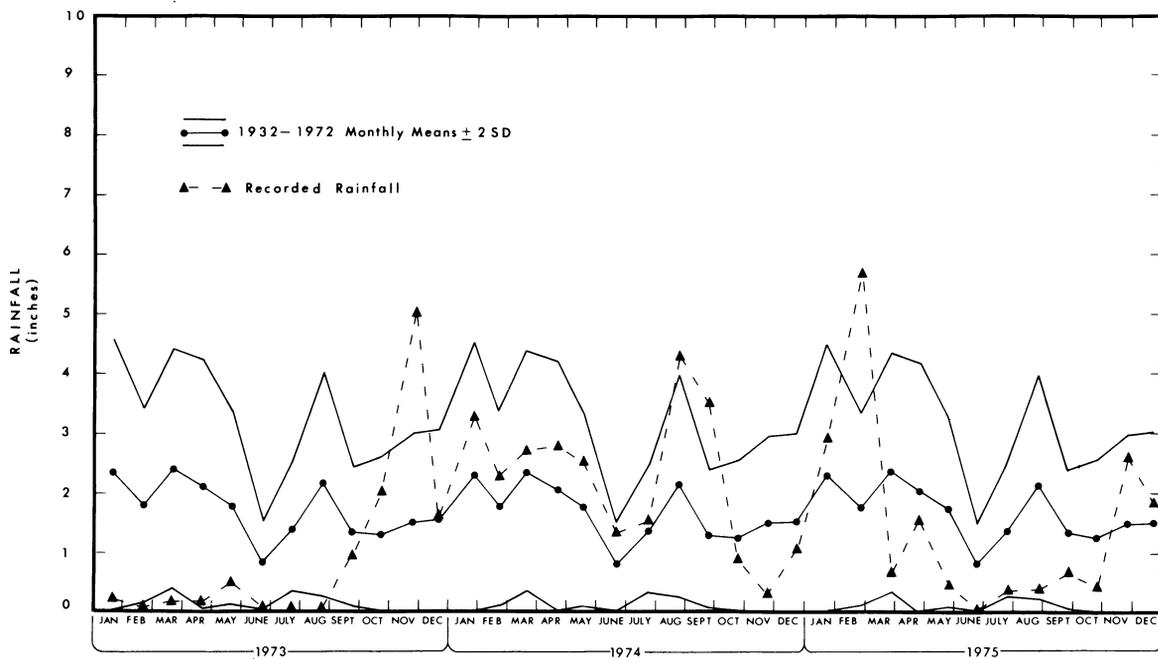


FIGURE 3. Mean precipitation over a 40-year period and recorded rainfall from 1973-1975 at Puu Laau on Mauna Kea, Hawaii.

and the variability in circumference of *Myoporum* among study sites was not significant.

of mature to immature trees for *Sophora* and *Myoporum* was determined for each relevé (table 1). When counting, all trees less than 2 m high were considered immature because they rarely produce

RATIO OF MATURE TO IMMATURE TREES.—The ratio

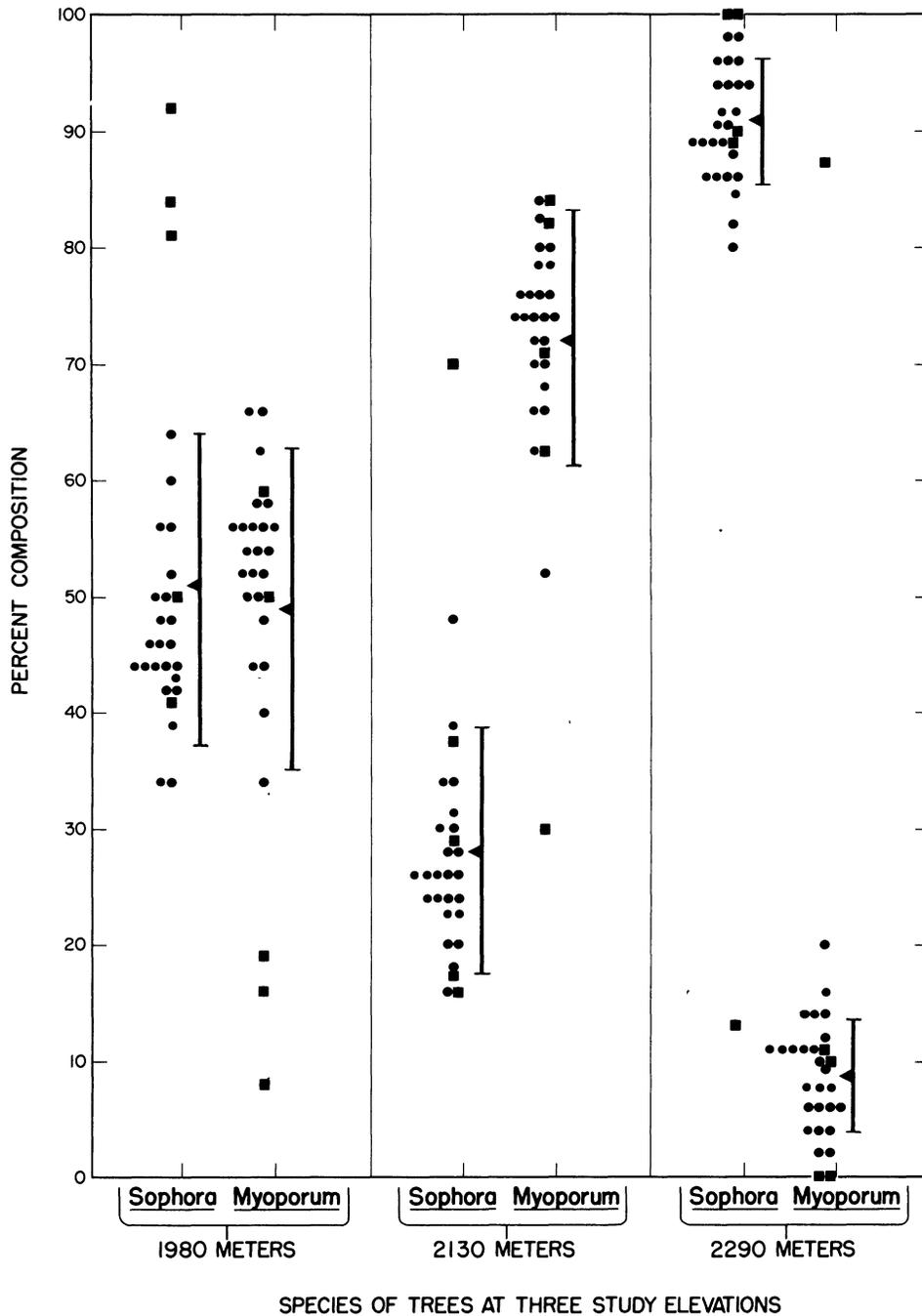


FIGURE 4. The percent forest composition of *Sophora chrysophylla* and *Myoporum sandwicense* at 1980 m, 2130 m, and 2290 m on Mauna Kea, Hawaii. Squares represent quadrat data, circles monthly walks through study sites; triangles are means, lines  $\pm 2$  SD.

flowers or fruit. The immature trees comprised 28.8 percent (26.5% *Sophora*; 2.3% *Myoporum*) of the forest at 1980 m, 20 percent (3.8% *Sophora*; 16.2% *Myoporum*) at 2130 m, and 30.2 percent (19% *Sophora*; 11.2% *Myoporum*) at 2290 m.

PHENOLOGY OF *Sophora*.—*Sophora* flowering was

TABLE 1. Number of mature (over 2 m) and immature (under 2 m) trees in relevé.

Elevation	Quad.	<i>Sophora</i>			<i>Myoporum</i>		Total	
		Mat.	Immat.	Mat.	Immat.	Mat.	Immat.	
1980 m	1	10	2	1	0	11	2	
	2	15	2	3	1	18	3	
	3	15	11	5	0	20	11	
	4	15	18	45	2	60	20	
	5	21	35	53	3	74	38	
2130 m	1	13	1	25	10	38	11	
	2	7	0	24	14	31	14	
	3	13	1	6	0	19	1	
	4	7	4	48	4	55	8	
	5	2	1	3	2	5	3	
2290 m	1	15	5	0	0	15	5	
	2	10	6	2	0	12	6	
	3	5	5	0	0	5	5	
	4	4	2	28	13	32	15	
	5	15	4	2	0	17	4	

TABLE 2. Mean tree height (in m) of mature *Sophora* and *Myoporum* on Mauna Kea, Hawaii. Parentheses indicate number of trees measured.

Relevé	1980 m		2130 m		2290 m	
	<i>Sophora</i>	<i>Myoporum</i>	<i>Sophora</i>	<i>Myoporum</i>	<i>Sophora</i>	<i>Myoporum</i>
1	6.6 (10)	8.7 (1)	6.2 (12)	6.4 (24)	7.1 (15)	— (0)
2	5.3 (14)	6.6 (3)	5.8 (6)	6.1 (20)	7.0 (10)	8.6 (2)
3	4.9 (15)	5.9 (5)	5.4 (14)	5.8 (6)	6.1 (5)	— (0)
4 <sup>a</sup>	5.5 (15)	5.7 (44)	6.3 (7)	6.5 (48)	(0)	(0)
5	4.9 (21)	5.5 (53)	5.0 (2)	5.5 (3)	7.3 (15)	6.2 (2)
Study Area	6.3 (10)	7.1 (6)	5.2 (8)	5.7 (42)	7.2 (47)	5.7 (3)
Average Mean Height	5.4	5.7	5.7	6.2	7.1	6.7

<sup>a</sup>The tree ratio in relevé four at 2290 m was unusual for the elevation, and when combined with other plot data created a biased composition; for this reason data were eliminated in calculations.

limited roughly to November through June, but a few widely scattered individuals with blossoms could be found during any month (fig. 5). Mature *Sophora* fruit followed flowering by three to four months in 1974 and by two to three months in 1975 (fig. 6). Generally, the intensity of flowering affected the amount of pod production: for example, in 1975 a tremendous blossom production at 1980 m gave rise to a large pod crop, while in 1974 at 1980 m a small amount of flowering yielded a small pod crop. Density of canopy or vegetative growth appeared to be influenced more by precipitation than by the time of year (fig. 7).

PHENOLOGY OF *Myoporum*.—Flowering occurred throughout most of 1974 with major blossom production during the dry period from April to August (fig. 8). This species fruited from May 1974 throughout May 1975, with very few fruits found during the six-month intervals before and after this period. In each year, inception of fruiting occurred first at either 2290 m or 1980 m (fig. 9). Vegetative growth occurred throughout the first part of the year, with canopy density greatest from May through August (fig. 10).

PRODUCTIVITY.—Productivity at each study site was calculated using formulas (1) and (2) in addition to data from intensity of flowering and fruiting of individual trees (table 4). *Sophora* usually produced about six times as many blossoms as pods. The fruits of *Myoporum* remain on the tree for a much longer

TABLE 3. Mean circumference at breast height (in cm) of mature *Sophora* and *Myoporum* on Mauna Kea, Hawaii. Parentheses indicate number of trees measured.

Relevé	1980 m		2130 m		2290 m	
	<i>Sophora</i>	<i>Myoporum</i>	<i>Sophora</i>	<i>Myoporum</i>	<i>Sophora</i>	<i>Myoporum</i>
1	60.7 (10)	71.1 (1)	65.5 (12)	40.4 (24)	92.7 (15)	— (0)
2	40.6 (15)	52.6 (3)	73.4 (6)	26.6 (20)	64.0 (10)	120.7 (2)
3	48.5 (15)	46.7 (5)	55.1 (9)	35.1 (6)	63.5 (5)	— (0)
4	— (0)	— (0)	— (0)	— (0)	68.1 (4)	41.1 (24)
5	— (0)	— (0)	36.8 (2)	72.9 (3)	64.0 (15)	43.2 (2)
Study Area	46.2 (10)	51.5 (6)	56.6 (8)	51.3 (42)	121.2 (47)	49.0 (3)
Average Mean Height	48.0	51.6	60.7	45.2	96.5	47.2

time period than do blossoms, a circumstance which accounts for the higher fruiting value at some locations. However, the closer similarity of *Myoporum* flower and drupe production indicates that this species has a higher seed set than does *Sophora*.

## DISCUSSION

The forest today on Mauna Kea is a unique ecosystem with *Sophora* and *Myoporum*, the two dominant tree species, utilizing different mechanisms of reproduction and responding differently to the same environ-

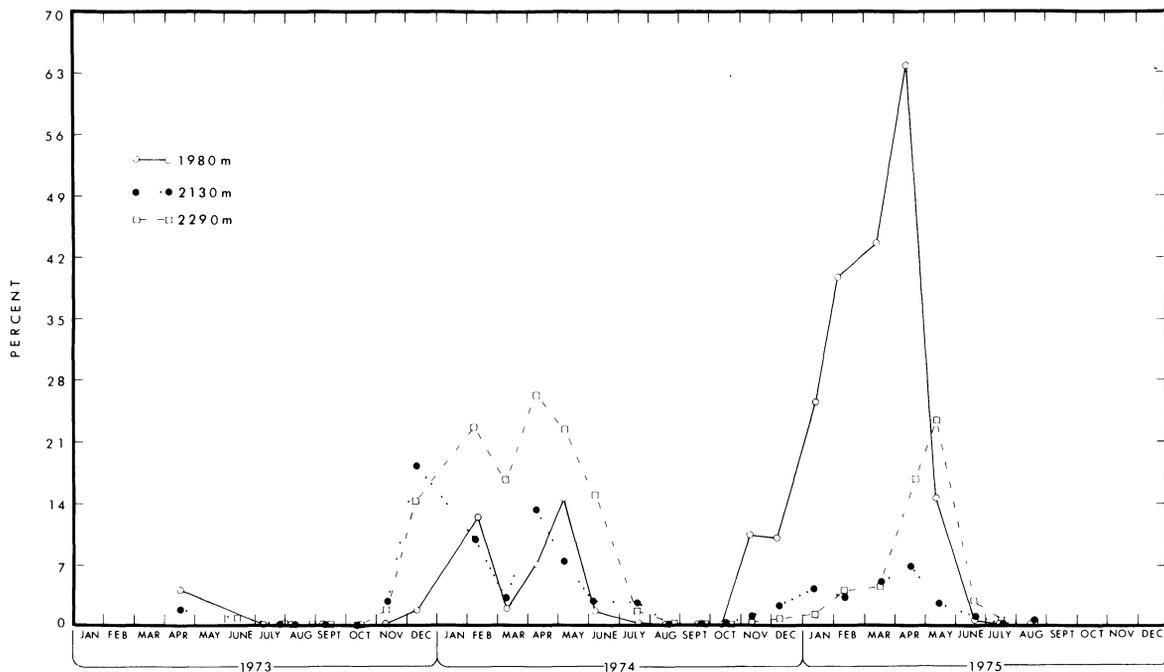


FIGURE 5. Percent of flowering per *Sophora chrysophylla* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

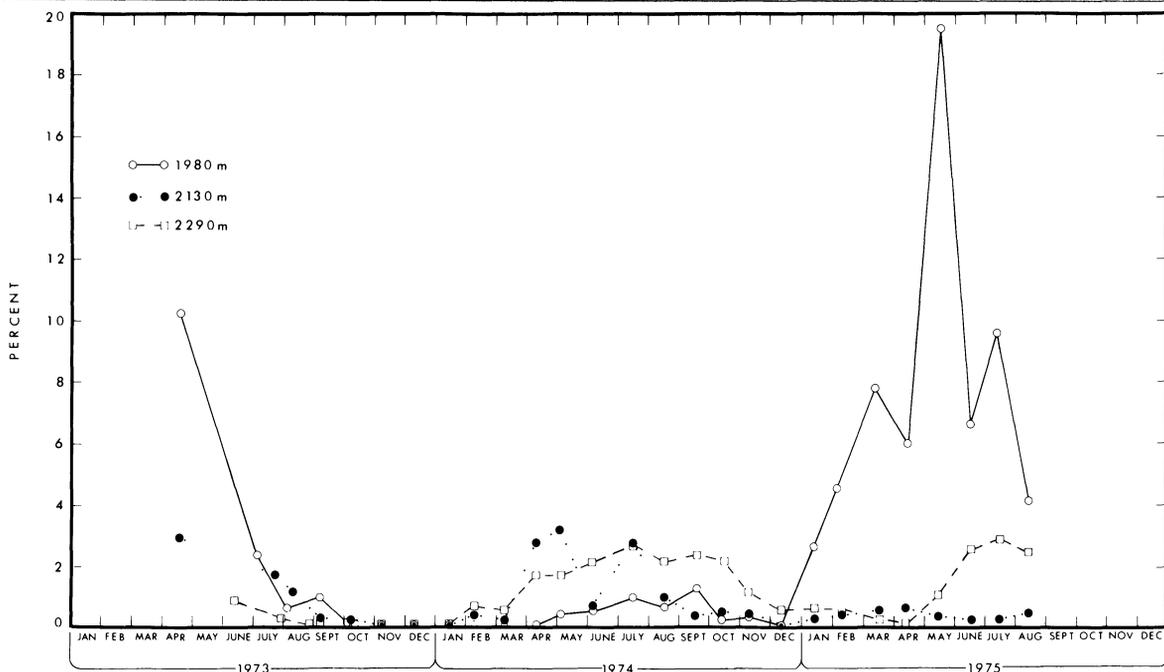


FIGURE 6. Percent of fruiting per *Sophora chrysophylla* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

mental conditions. What appears most important, however, is the inability of *Sophora* to cope with the browsing pressure exerted by introduced feral sheep (Giffin 1976). To understand the ecology of this area, abiotic as well as biotic factors must be con-

sidered in terms of their combined pressure on the forest.

It is evident that forest composition of Mauna Kea has changed dramatically over recent years. At one time the area must have been composed of a

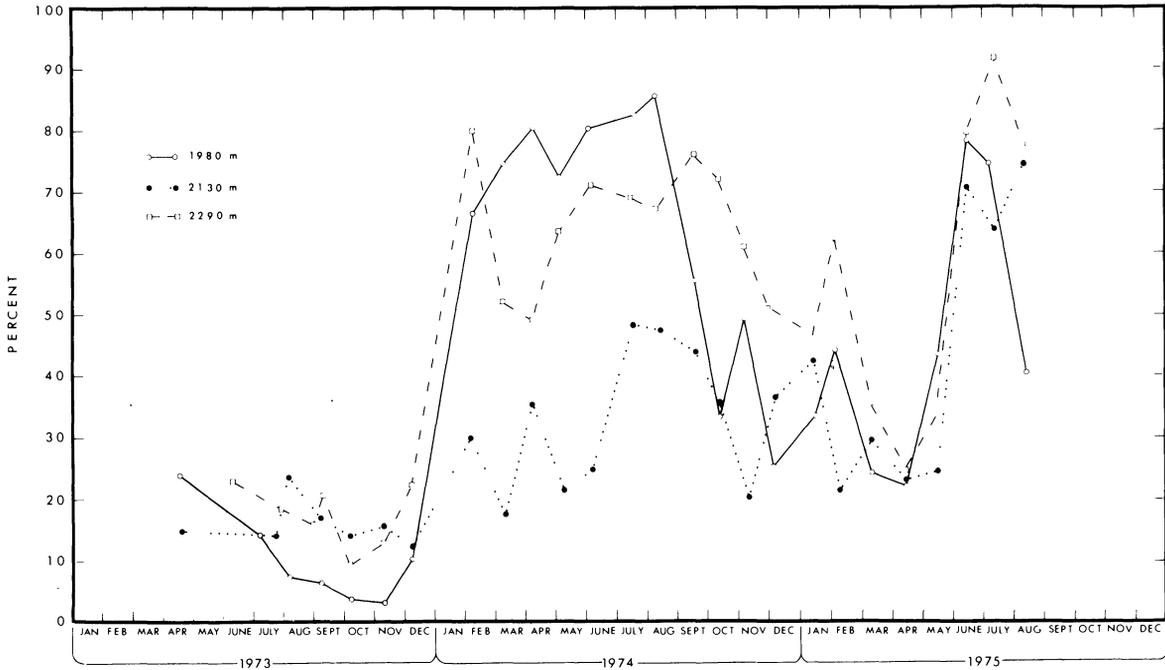


FIGURE 7. Percent of canopy cover per *Sophora chrysophylla* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

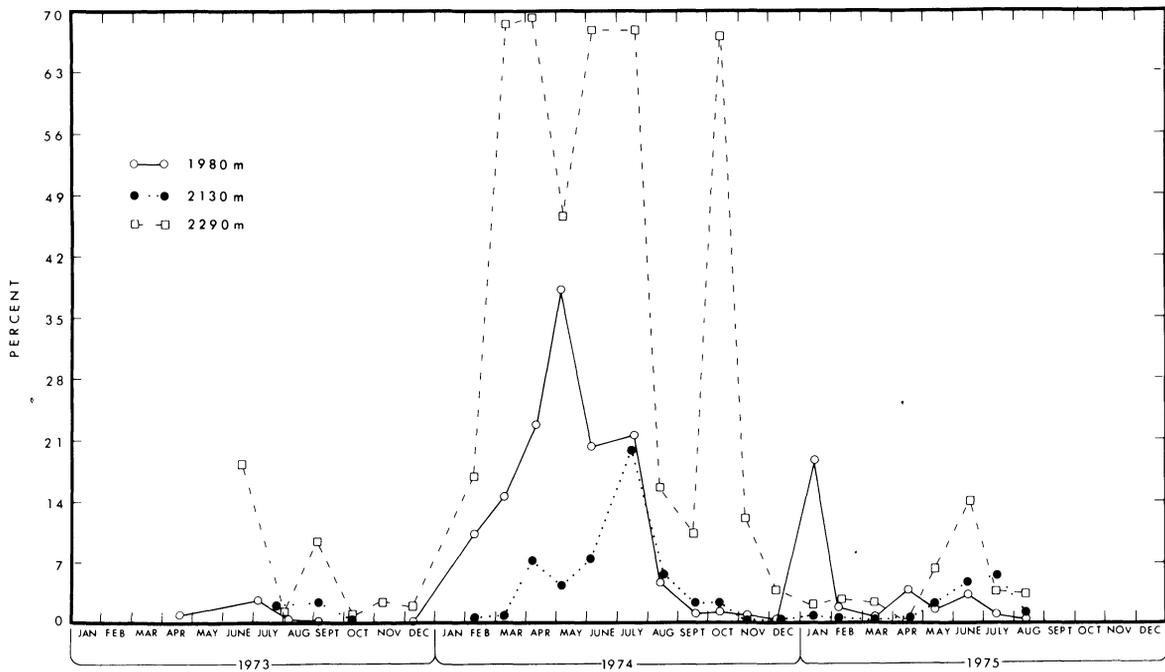


FIGURE 8. Percent of flowering per *Myoporum sandwicense* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

variety of trees, as small remnant pockets of these now rare species can be found scattered around the mountain. *Santalum* was cut extensively for export (Rock 1913); *Euphorbia* is restricted to rocky out-

crops; and *Dubautia* is found only on the sides of steep gullies, where sheep and cattle cannot reach it. Because *Myoporum* is not a preferred browse species, the trend in the forest today is for the tree to in-

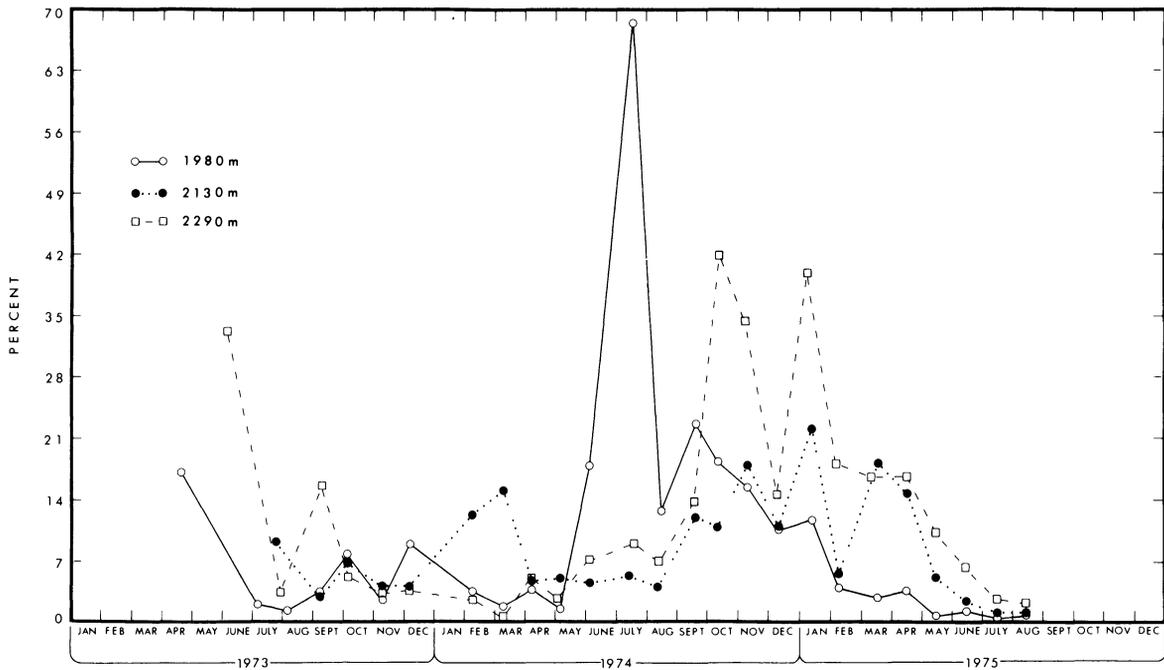


FIGURE 9. Percent of fruiting per *Myoporum sandwicense* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

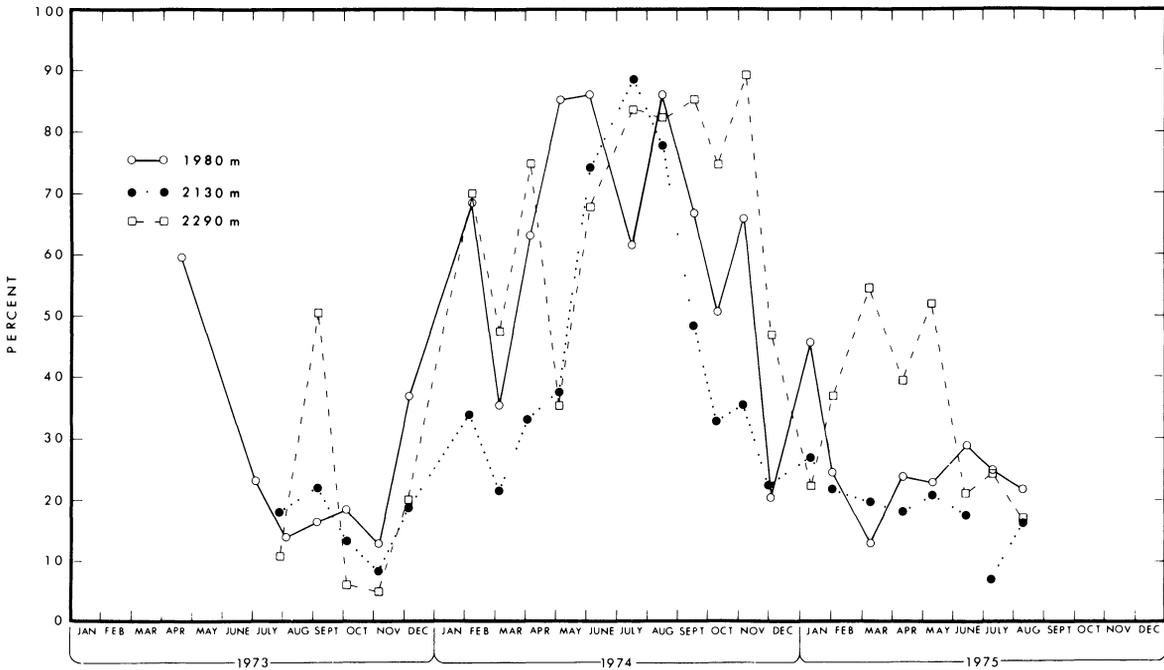


FIGURE 10. Percent of canopy cover per *Myoporum sandwicense* tree from 1973-1975 in study relevés on Mauna Kea, Hawaii.

crease in numbers. This effect is shown by the much higher proportion of *Sophora* in the 2290 m study plot than at higher elevations on the southern slope of Mauna Kea where feral sheep browsing pressure is greater (pers. obs.). Moreover, the 2290 m study area was a fenced enclosure where feral sheep could no longer browse, and it had the highest young-to-adult *Sophora* ratio occurring at that elevation. The remaining two study areas were near roads, and because of hunting pressure sheep flocks visited them infrequently.

TABLE 4. Productivity index for flowering and fruiting of *Sophora* and *Myoporum* on Mauna Kea, Hawaii.

Species	Elevation	1974		1975	
		Flower	Fruit	Flower	Fruit
<i>Sophora</i>	1980	182.3	12.6	786.0	241.0
	2130	153.9	26.1	72.9	10.3
	2290	423.8	72.5	293.0	56.6
<i>Myoporum</i>	1980	549.3	711.0	178.3	164.3
	2130	201.3	408.7	83.8	393.6
	2290	596.6	167.9	62.2	187.7

Taking into account productivity values and the ratio of young to adult trees (tables 1, 4), *Sophora* and *Myoporum* appear to have a similar reproductive potential. Given an environment free of browsing pressure, *Sophora* could compete successfully with *Myoporum*. However, there still remains considerable browsing pressure on Mauna Kea, and Giffin (1976) found that in a region where both tree species were in approximately equal abundance, *Sophora* comprised over 20 percent of the sheep's diet whereas *Myoporum* comprised only 0.1 percent. This observation may explain why the composition of the forest, especially on the southern slope of the mountain at tree line, has changed so radically. *Myoporum* is a pioneer species (see also the discussion by Cooray 1974); when *Sophora* trees die, *Myoporum* fills the vacant areas rapidly. In a normal sequence of events, *Sophora* would eventually replace *Myoporum*, but with selected browsing pressure against *Sophora*, *Myoporum* is able to persist and is now the only species that remains in some of these more remote areas.

Aside from the pressures exerted by introduced mammals, the most pervading and proximate influences upon the flora of Mauna Kea are abiotic factors. It is interesting that within only a 300 m elevational rise, tree-species composition changed dramatically within the study sites (fig. 4). Differences in soil

characteristics may have accounted for this because the 2130 m site had a larger number of rock outcrops, and the soil is classed as 'stony' (Sato *et al.* 1973); the 1980 and 2290 m study sites had much deeper and less stony soil. *Sophora* numbers were lowest at the 2130 m site as were values for flowering and fruiting productivity. *Sophora* may, therefore, need a greater soil depth in order to maximize reproduction.

Although the percent composition differed among elevations, tree density remained constant. This situation suggests that some controlling factor (e.g., water) limits the number of trees (regardless of species) per unit area of ground. Drainage conditions may also be important, although all three study locations had similar 12 to 20 percent slopes.

*Sophora* and *Myoporum* responded differently to the yearly weather pattern, but both were well adapted for successful pollination and seed dispersal. *Sophora* has large conspicuous flowers with quantities of nectar; this situation usually indicates that birds are the primary pollinators (Wolf *et al.* 1972). I have observed *Vestiaria coccinea* migrate into the forest during the early flowering period (December-January) and establish feeding territories at flowering *Sophora* trees. The peak bloom period of *Sophora* also occurs when *Loxops virens* populations are at their greatest density (van Riper 1978), and this bird is probably the primary species responsible for pollination. The grey-green foreheads and crowns of juvenile *L. virens* are often so covered with *Sophora* pollen that they appear yellow. *Myoporum*, on the other hand, flowers after *L. virens* populations have dispersed. The blossoms of this tree are small and inconspicuous, and I have rarely observed *L. virens* feeding on them. It appears that this tree relies upon wind or insects for pollination, but this hypothesis remains to be documented.

The physical appearance of *Sophora* and *Myoporum* fruit differs considerably. *Sophora* has a thick outer covering that is very hard when mature, and the seeds are viable over extended periods of time (Akamine 1951). Such a dormancy mechanism may prevent germination in the dry season, during which an adequate root system could not develop. *Sophora* seeds are eaten principally by *Psittirostra baillieui*, and there is evidence that this bird acts as a disperser by carrying partially eaten pods to areas away from the parent tree (van Riper 1980). *Myoporum* fruit, on the other hand, is moist and fleshy, and is taken by a variety of avian species (van Riper 1975). It is a common pattern for dryforest trees to fruit in the dry season (Daubenmire 1972, Hopkins 1970, Richards 1952), with the presumptive advantage that fruit is readily taken by birds for its moisture content.

Presently, a number of birds newly introduced to Hawaii eat *Myoporum* fruits, e.g., Red-billed Leiothrix (*Leiothrix lutea*); House Finch (*Carpodacus mexicanus*); Turkey (*Meleagris gallapavo*). Some of these seed dispersers might be contributing to the recent expansion of *Myoporum*.

## ACKNOWLEDGEMENTS

My special appreciation to A. J. Berger and C. H. Lamoureux for their critical analysis and suggestions throughout

this study. I have benefited from helpful comments offered by H. G. Baker, S. G. van Riper, C. J. and C. P. Ralph, R. A. Kinzie III, P. Scowcroft, and C. W. Smith on various drafts of this manuscript. Assistance of S. Monden with illustrations and D. Reeser with logistics is also appreciated. For the use of their facilities during this investigation I thank J. Giffin, E. Kosaka, R. and S. Johnston, S. Landsberg, J. Spencer, and especially J. Q. and I. Casey. Financial support was provided in part by the Frank M. Chapman Memorial Fund, World Wildlife Fund Grant US-35, and CX 8000-7-0009 from the National Park Service to the Cooperative National Park Resources Studies Unit at the University of Hawaii.

---

## LITERATURE CITED

- AKAMINE, E. K. 1951. Viability of Hawaiian forest tree seeds in storage at various temperatures and relative humidities. *Pacif. Sci.* 5: 36-46.
- COORAY, R. G. 1974. Stand structure of a montane rain forest on Mauna Loa, Hawaii. IBP Island Ecosystems IRP Tech. Rep. No. 44.
- DAUBENMIRE, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. *J. Ecol.* 60: 147-170.
- FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881-913.
- GIFFIN, J. G. 1976. Ecology of the feral sheep on Mauna Kea. Pittman-Robertson Project No. W-15-5, Study No. XI. 1972-75. Dept. Land and Natural Resources, Division of Fish and Game, Honolulu.
- HART, C. E., AND M. C. NEAL. 1940. The plant ecology of Mauna Kea, Hawaii. *Ecology* 21: 237-266.
- HOPKINS, B. 1970. Vegetation of the Olokemeji Forest Reserve, Nigeria. VI. The plants on the forest site with special reference to their seasonal growth. *J. Ecol.* 58: 765-793.
- LAMOUREUX, C. H. 1973. Phenology and growth of Hawaiian plants, a preliminary report. IBP Island Ecosystems IRP Tech. Rep. No. 24.
- RICHARDS, P. W. 1952. The tropical rain forest: An ecological study. Cambridge Univ. Press, London.
- ROCK, J. F. 1913. The indigenous trees of the Hawaiian Islands. Publ. under patronage. Reprinted in 1974 by Chas. E. Tuttle Co., Inc. Tokyo, Japan.
- SATO, H. H., W. IKEDA, R. PAETH, R. SMYTHE, AND M. TAKEHIRO, JR. 1973. Soil survey of the island of Hawaii, State of Hawaii. U.S. Soil Conservation Service in cooperation with Univ. of Hawaii Agric. Exp. Sta.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. Iowa State Univ. Press, Ames, Iowa.
- VAN RIPER, C., III. 1975. The phenology of mamane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) on Mauna Kea, Hawaii, as related to the annual cycle of the Amakihi (*Loxops virens*) and the Palila (*Psittirostra bailleui*). IBP Island Ecosystems IRP Tech. Rept. No. 51.
- . 1978. The breeding ecology of the Amakihi (*Loxops virens*) and Palila (*Psittirostra bailleui*) on Mauna Kea, Hawaii. Ph.D. Dissertation. Univ. of Hawaii, Honolulu.
- . 1980. Observations on the breeding of the Palila *Psittirostra bailleui* of Hawaii. *Ibis* 122: 462-475.
- WARNER, R. E. 1960. A forest dies on Mauna Kea. *Pacif. Discovery* 13: 6-14.
- WOLF, L. L., F. R. HAINSWORTH, AND F. G. STILES. 1972. Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. *Science*, N.Y. 176: 1351-1352.